

BREEDING BIOLOGY AND FOOD HABITS OF THE MADAGASCAR KESTREL (*FALCO NEWTONI*) IN NORTHEASTERN MADAGASCAR

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ABSTRACT.—We studied Madagascar Kestrels (*Falco newtoni*) on Masoala Peninsula, northeastern Madagascar during the 1997 and 1998 breeding seasons. We located five nest sites and observed eight nesting attempts during the two breeding seasons. All nests were in tree cavities and averaged 13.8 ± 2.0 m (SE) above the ground in trees averaging 22.8 ± 0.8 m (SE) in height ($N = 5$ nests). Egg laying took place from mid-September to the first week of October. The modal clutch size was 4 ± 0.9 ($N = 6$ nests, range 3–5 eggs). The incubation period averaged 28 d, varying from 27–29 d ($N = 5$ nests). Hatching occurred from the middle of October to the first week of November with young fledging in late November. Of 24 eggs laid in six nests, 13 (54%) hatched, and seven (54%) of those hatchlings fledged; thus, a total of 1.2 young fledged per breeding attempt were produced and overall nest success was 50%. The Madagascar Kestrel diet of 338 identified prey was composed of 93.8% lizards ($N = 317$), 2.6% insects ($N = 9$), 2.4% amphibians ($N = 8$), and 1.2% birds ($N = 4$).

KEY WORDS: *Madagascar Kestrel; Falco newtoni; nesting biology; food habits; nests; productivity.*

BIOLOGÍA REPRODUCTIVA Y HÁBITOS ALIMENTICIOS DE *FALCO NEWTONI* EN EL NORESTE DE MADAGASCAR

RESUMEN.—Estudiamos individuos de la especie *Falco newtoni* en la península Masoala en el noreste de Madagascar durante las estaciones reproductivas de 1997 y 1998. Localizamos cinco nidos y observamos ocho intentos de nidificación durante los dos periodos reproductivos. Todos los nidos se encontraron en cavidades en árboles a una altura promedio de 13.8 ± 2.0 m (EE) sobre el suelo y en árboles con una altura promedio de 22.8 ± 0.8 m (EE) ($N = 5$ nidos). La puesta de huevos ocurrió desde mediados de septiembre hasta la primera semana de octubre. El tamaño modal de la nidada fue de 4 ± 0.9 huevos ($N = 6$ nidos, rango 3–5 huevos). El período promedio de incubación fue de 28 días, variando entre 27–29 días ($N = 5$ nidos). La eclosión ocurrió desde mediados de octubre hasta la primera semana de noviembre y el abandono del nido por parte de los polluelos ocurrió a fines de noviembre. De los 24 huevos puestos en seis nidos, 13 (54%) eclosionaron, y siete (54%) de los polluelos que eclosionaron abandonaron el nido. Por lo tanto, se produjeron un total de 1.2 juveniles que abandonaron el nido por intento de nidificación, y el éxito de nidificación general fue del 50%. La dieta de *F. newtoni*, basada en 338 presas identificadas, estuvo compuesta en un 93.8% por lagartijas ($N = 317$), en un 2.6% por insectos ($N = 9$), en un 2.4% por anfibios ($N = 8$) y en un 1.2% por aves ($N = 4$).

[Traducción del equipo editorial]

Madagascar has three resident species of falcons: Madagascar Kestrel (*Falco newtoni newtoni*), Banded Kestrel (*F. zoniventris*), and Peregrine Falcon (*F. peregrinus radama*), and two wintering species, Eleonora's Falcon (*F. eleonora*) and Sooty Falcon (*F. concolor*). Although the Madagascar Kestrel is the

most common raptor in Madagascar (Siegfried and Frost 1970), detailed information on its biology and natural history are lacking (Langrand and Meyburg 1984, Langrand 1990). This species is widely distributed throughout Madagascar and is found in open grasslands, savannah habitat, degraded forests, and in the vicinity of villages and towns. This falcon has two distinctive color morphs: pale and rufous (Siegfried and Frost 1970,

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Cade 1982, Langrand 1990). In this paper, we report basic information on the breeding biology and food habits of the Madagascar Kestrel.

STUDY AREA AND METHODS

This study was conducted within the secondary habitat and cultivated terrain surrounding Ambanizana Village (49°57'E, 15°37'S), situated at the western boundary of the Masoala National Park (MNP; Robenarimangason 1999).

Most of the peripheral zones of the MNP, are composed of degraded forest, secondary forest, and fallow land intermixed with cultivated areas (crops include cloves, coffee, vanilla, and bananas). The MNP itself consists of 230 000 ha of primary forest with a typical canopy height of 25 m and with some emergent trees exceeding 30 m (Guillaumet 1984). The forested terrain is mountainous, and lacks roads and a trail system. The altitude in the park ranges from sea level to 1230 m (Nicoll and Langrand 1989). The current study was undertaken in the lower altitude and cultivated areas ranging from sea level to 200 m above sea level. The annual mean rainfall at Andranobe Field Station, 7 km south of the study site, is 6049 mm (Thorstrom et al. 1997). The dry season is from October to mid-December (Rene de Roland 2000). The climate is mild and the annual mean temperature varies from 18–31°C.

The study period was from September 1997–January 1998 and September 1998–January 1999, which coincides with the kestrel's breeding season. During September and October, we searched for nesting pairs by following vocalizing and flying adults. Observations were made at least 50 m from nests, and five and three nests were monitored during the 1997 and 1998 breeding seasons, respectively.

Nests were observed from courtship up to post-fledgling period, and 521 hr 22 min of observation were completed. We recorded copulation frequency (per hr and d) and duration (sec), clutch size (number), incubation period (d), nest attendance (percent of observation time), dispersal of young (d), and productivity. Egg dimensions (length and breadth), and egg and nestling mass were measured using vernier calipers (with 0.01 mm of precision) and Pesola spring-balance scales (0.1 g precision), respectively. Daily nest observations were made from 0600–1800 H with 10× binoculars and a zoom spotting scope. While making observations at nests prey items were identified during prey deliveries.

Kestrels were trapped with a bal-chatri, a noose carpet fixed over the nest entrance, or a "wire hoop trap" (Berger and Mueller 1959, Thorstrom 1996). Morphometric measurements taken were: wing chord (mm), tail and tarsi length (mm), and body mass (g). One breeding pair of adult kestrels was radiotagged to estimate their ranging area. The kestrels were radio-tracked from October–December 1998 by homing on foot, and locational fixes were recorded using an Eagle Explorer Global Position System (GPS; Eagle Electronics, Catoosa, OK U.S.A.) with 30-m of accuracy. The home range was estimated by the minimum convex polygon (MCP) of the locations using Ranges IV software (Kenward 1990). Several nest site parameters (i.e., nest height, nest tree height, nest dimen-

sions, nest depth, and internest distance) were measured after the young had fledged.

RESULTS

One pair of Madagascar Kestrels was trapped and marked during this study. The adult female measurements were wing chord, 200 mm; tail length, 129 mm; tarsus length, 38.2 mm; and body mass, 122 g. The adult male measurements were wing chord, 195 mm; tail length, 110.5 mm; tarsus length, 37.0 mm; and body mass, 110 g.

Five nesting attempts were observed during the first season, 1997–98, and three were documented during the second field session, 1998–99. Of the five nesting pairs observed during the two breeding seasons, three pairs were composed of a pale-morph male and a rufous-morph female, one pair was of a rufous-morph male paired with a pale-morph female, and one pair included both rufous-morph individuals.

Nest Characteristics. During this study, all nests observed for Madagascar Kestrels were placed in natural-tree cavities, with a decayed wood substrate, in secondary and human-modified habitat. The trees identified for nesting were mandrorofo (*Trachylobium rerrucosum*), hintsia (*Afzelia bijuga*), lalona (*Weinmania* sp.), and dead unidentified snags. Madagascar Kestrel nests averaged 13.8 ± 4.5 m ($N = 5$) above the ground in trees averaging 22.8 ± 1.9 m ($N = 5$) in height. Nest cavities were oval-shaped and measured 61 ± 55.1 cm ($N = 2$) by 33.5 ± 16.2 cm ($N = 2$) with an interior depth of 22.5 ± 3.5 cm ($N = 2$). The distance between two neighboring nests averaged 675 ± 386.2 m ($N = 4$, range 300–1200 m).

Nesting Biology. Courtship activity involved vocalizations, nest site visits with food deliveries to the female, and copulations. The courtship period was marked by flights (e.g., in open areas and over trees) and accompanied by moderate fluttering of wings. During periods of inactivity, the kestrel pair perched together in the top of dead branches of trees. Courtship behavior, either flights or periods of inactivity, was associated with loud calls "itsi, kitsi, kitsi, kitsi." During this period, the male's primary role seemed to be showing the female potential nesting sites.

Copulations usually occurred after prey deliveries from the male to the female. Copulations occurred on the top of dead branches. During copulations, the male emitted a "iiitsi, kitsi, kitsi, kitsi. . ." that continued to the end of this activity.

Table 1. Number of prey items delivered by male and female Madagascar Kestrels at Masoala Peninsula, Madagascar, during the breeding seasons of 1997 and 1998.

SEX	COURTSHIP	INCUBATION	NESTLING	POST-FLEDGING	TOTAL
Male	13	110	130	18	271
Female	0	0	28	39	67
Total	13	110	158	57	338

The highest frequency of copulations during a 1 hr period occurred between 0600–0700 H ($N = 13$ of 91 observed copulations). Copulations were also frequent during the 0800–1000 H ($N = 28$) and 1300–1500 H ($N = 28$). Ten days prior to the onset of incubation, the frequency of copulations averaged 9.1 ± 0.4 (SE) times per day ($N = 91$ copulations, range 7–11). Copulations averaged 4.9 ± 1.6 sec in duration ($N = 44$, range 3–8 sec). Three copulation attempts were also observed during the late incubation and nestling period.

Egg laying took place from mid-September to the first week of October. The earliest egg was laid on 18 September 1997 and the latest was on 5 October 1997. The mean clutch size was 4.0 ± 0.9 ($N = 6$ nests, range 3–5 eggs). Eggs measured $33.9 \text{ mm} \pm 0.9 \text{ mm} \times 28 \text{ mm} \pm 0.6 \text{ mm}$ and their mass was $14.3 \pm 0.6 \text{ g}$ ($N = 5$ eggs) during the first week of incubation. Eggs were pale white with dark brown spots.

Constant incubation seemed to be initiated following the laying of the second egg. The incubation period averaged 28 d and varied from 27–29 d ($N = 5$ nests: 27 d [$N = 3$], 29 d [$N = 2$]). Incubation was done by females only, and they incubated for 88.5% of the observation time and were absent for 11.5% of the time ($N = 153.1$ hr). The male's responsibility during this period was providing food to the incubating female. Prey exchanges occurred on branches of trees neighboring the nest tree.

Nestling and Fledgling Period. Up to 6 d of age, the young were constantly brooded by the female (96.5% of the observation time [$N = 20.7$ hr]). Brooding progressively decreased to 38.7% just prior to the time of fledging. Young were fed solely by the female until about 15 d of age when they were able to feed themselves, were active in the nest, and completely covered with contour feathers. After about 15 d of age, prey delivered by the adults was dropped into the nest cavity from the entrance. Both the male and female provisioned the young with food during the nestling period

(Table 1). During this period, the adult female was very aggressive toward other cavity-nesting birds (e.g., Madagascar Starlings [*Hartlaubius aurata*] and Broad-billed Rollers [*Eurystomus glaucurus*]), and occasionally attacked them.

Nestlings were observed wing exercising at the cavity entrance at 3 wk of age. Two to three days before fledging, two males weighed 112 g and 118 g, and one female was 128 g. Young fledged at 23–24 d of age ($N = 7$ young). After fledging, the young were observed perching together in trees close to the nest tree. During the second week after fledging, they were observed catching insects and attacking prey, and the prey delivery rate by adults decreased progressively. Young dispersed from their natal areas at 44–45 d of age ($N = 7$ young).

Reproductive Success. In six fully-documented nests containing 24 eggs, 13 (54%) eggs hatched and 7 (54%) of the hatched young fledged. In total, seven young fledged from three successful breeding attempts, for a productivity of 2.3 young fledged per successful nest. Overall productivity was 1.2 (7/6 pairs) young per nesting pair. Nest success for the 2 yr of this study was 50% (3/6 pairs; Table 2).

In the six nesting attempts during the two breeding seasons, one nest failure occurred during incubation and two during the nestling period. In 1997, we believe one nest failed during incubation due to nest competition with a pair of Broad-billed Rollers for the cavity, and the nest was abandoned by the kestrel pair prior to hatching. In another instance in 1997, three nestlings were killed and partially eaten by an unknown predator. In 1998, one nest failed when the eggs were eaten and another nest failed during an intense 5-d rain storm when the nestlings were found dead in and below the nest, possibly due to lack of sufficient brooding by the adult female or due to water in the nest cavity.

Food Habits. Madagascar Kestrels used different hunting strategies, including hovering flight and perch hunting. Prey on the ground was hunted

Table 2. Reproductive success of six fully-documented breeding attempts of the Madagascar Kestrel (*Falco newtoni*) during 1997 and 1998 at Masoala Peninsula, Madagascar.

YEAR	BREEDING ATTEMPTS	NUMBER OF EGGS	MEAN CLUTCH SIZE	NUMBER EGGS HATCHED (%)	NUMBER OF YOUNG FLEDGED (%)	FLEDGLINGS/BREEDING ATTEMPTS	NEST SUCCESS PERCENT (N)
1997	4	16	4	10 (63)	4 (40)	1.0 (4/4)	50 (4)
1998	2	8	4	3 (38)	3 (100)	1.5 (3/2)	50 (2)
Total	6	24	4	13 (54)	7 (54)	1.2 (7/6)	50 (6)

from the air by stationary flight or “hovering,” ending in the kestrel plunging down and capturing the prey. The second method was scanning for prey from a high lookout, usually from a tree. Once prey was located, kestrels bobbed their heads several times as if sighting in on the prey before gliding down to seize their quarry. During the two study seasons, 1997 and 1998, we recorded 370 Madagascar Kestrel prey items, mainly those brought to nests; 338 were identified. Plated lizards (*Zonosaurus brygooi* and *Z. madagascariensis*) comprised 93.8% ($N = 317$), insects 2.6% ($N = 9$), amphibians 2.4% ($N = 8$), and birds 1.2% ($N = 4$). Adult males and females delivered different quantities of prey during the different breeding periods (Table 2). In total, of 338 identified prey, 80.2% ($N = 271$) and 19.8% ($N = 67$) were delivered by males and females, respectively.

During the 1998 breeding season, one nesting pair of radio-tagged kestrels had an estimated MCP home range of 25.6 ha ($N = 30$ locational fixes).

DISCUSSION

The Madagascar Kestrel is considered to be one of the most common and widespread raptor species throughout Madagascar (Rand 1936, Siegfried and Frost 1970, Langrand and Meyburg 1984). Ferguson-Lees and Christie (2001) stated “. . .this is probably the only Malagasy raptor to have gained from deforestation, and is clearly under no threat.” This species appears to be benefiting from deforestation (Langrand and Meyburg 1984), and on the Masoala Peninsula, kestrels are occupying openings, secondary and human-modified habitats adjacent to intact forest fragments and the primary forest (Rene de Roland 1994).

Cade (1982) commented that Madagascar Kestrels show more pronounced sexual-size dimorphism in comparison to most kestrel species based on work by Siegfried and Frost (1970), who reported males averaging 72.9% of female mass

(males averaged 105 g [90–117 g, $N = 4$] and females averaged 144 [131–153 g, $N = 7$]). We were not able to document the extent of sexual dimorphism, as we measured only one pair, and in this single instance the male was 90% of the female’s mass.

All nests found in this study were situated in natural-tree cavities. All cavities seemed to have developed through decay, where a limb had broken or the tree’s heartwood had a rotten opening the interior. Langrand (1990) reported that Madagascar Kestrel nests can also be found in cliff holes, under house roofs, and infrequently in old nests of other avian species. The Seychelles Kestrel (*F. araea*) and Mauritius Kestrels (*F. punctatus*) are known to use tree cavities for nesting and also potholes in cliff faces (Temple 1977, Cade 1982, Watson 1992). On Masoala Peninsula, rocky and potholed cliff faces are extremely rare and are unavailable for nesting sites for Madagascar Kestrels.

In the central plateau region of Madagascar, this species is known to occupy buildings for nesting as is the Seychelles Kestrel (Watson 1992). However, on the Masoala Peninsula humans are recent inhabitants in this region and large suitable buildings for nesting kestrels are nonexistent. In southwestern Madagascar, kestrels occupy abandoned nests of other birds (e.g., Pied Crow [*Corvus albus*]; Rene de Roland pers. obs.). In the northeastern region, old stick nests are built (and usually occupied) by larger raptors inside forested habitat, and this tends to exclude kestrels from using this type of nesting structure. Consequently, the human degradation of forested habitat on Masoala Peninsula has left isolated trees for nesting habitat for Madagascar Kestrels. Madagascar Kestrels do not seem to be highly selective in regard to tree species or nest height they use, but are dependent on the availability of suitable tree cavities within the human-modified habitat. On Masoala Peninsula, cav-

ity nesting by Madagascar Kestrels differed markedly from sympatric Banded Kestrels, which placed their nests only inside arboreal-epiphytic ferns (Thorstrom 1999, Rene de Roland et al. 2005).

During research conducted on raptors on Masoala Peninsula from 1991–97, no Madagascar Kestrels were found nesting inside the intact primary forest (Rene de Roland 1994, Robenarimangason 1999, Thorstrom and Rene de Roland 2000). In contrast, the Mauritius Kestrel and Seychelles Kestrel did occupy and nest in dense forests, forest fragments and secondary forest patches (Cade 1982, Watson 1992, Cade and Jones 1993).

Most of the breeding biology of this species follows the usual kestrel pattern and behavior, but there are some exceptions. For instance, the courtship period is marked by a distinct flight consisting of a series of climbs and dives with continuous powerful wing beats as seen in American Kestrels (*F. sparverius*; Willoughby and Cade 1964) and European Kestrels (*F. tinnunculus*; Brown and Amadon 1968), but we did not observe such courtship flights for Madagascar Kestrels or the sympatric Banded Kestrels in this region (Rene de Roland et al. 2005). Seychelles Kestrels do not display this specialized courtship flight either (Vesey-Fitzgerald 1940). Both sexes of Madagascar Kestrels, Banded Kestrels, as well as the Seychelles Kestrel do emit specific vocalizations during the courtship period (Watson 1993, Rene de Roland et al. 2005). The copulation duration of 5 sec (range 3–8 sec) for the Madagascar Kestrel was slightly shorter than the sympatric Banded Kestrel with a mean near 8 sec (range of 5–10 sec; Rene de Roland et al. 2005).

Newton (1979) noted that the eggs of smaller raptor species are laid every couple of days, but in this study we observed Madagascar Kestrels laying eggs daily. At one nest in 1997, five eggs were laid on five consecutive days. The fresh egg masses for Seychelles Kestrels, 12.4 g or 14% of mean female body mass ($N = 10$ eggs; Watson 1993) and American Kestrels, 13.8 g or 11.2% of mean female body mass ($N = 53$ eggs; Balgooyen 1976) are comparable to those of Madagascar Kestrels (14.3 g or 10% of female body mass) from this study.

Cade (1960) noted that the genus *Falco* requires 28–30 d of incubation. The incubation period for Seychelles Kestrels was 28–31 d (Watson 1992), for Mauritius Kestrels about 30 d (Cade 1982), and we found a similar period for the Madagascar Kestrel ranging from 27–29 d.

Like Seychelles Kestrels (Watson 1993) and Mauritius Kestrels (Cade 1982), both female and male Madagascar Kestrels contributed to prey provisioning during the nestling period. Madagascar Kestrels dropped prey into the nest cavity during the latter stage of the nestling period, and this has also been observed in American Kestrels (Balgooyen 1976). Madagascar Kestrels were most aggressive against other cavity nesters during the nestling period, and this has been observed with other kestrel species (Balgooyen 1976).

Madagascar Kestrels fledged at 23–24 d of age, much earlier than Seychelles Kestrels at 35–42 d (Watson 1993) and Mauritius Kestrels at 38–39 d (Cade 1982). The shorter nestling period for Madagascar Kestrels might be attributed to their adaptation to nesting in open habitat, whereas the protracted breeding season of the Mauritius and Seychelles kestrels are adapted to tropical forested situations (Cade 1982, Watson 1992).

Adult Madagascar Kestrels continued to use the nest for prey deliveries to the fledglings. Young Madagascar Kestrels caught prey by 14 d after fledging and young American Kestrels also were successful in catching prey at 12–14 d after fledging (Balgooyen 1976). The prey delivered by adult Madagascar Kestrels decreased progressively during the post-fledgling period until young dispersed and were independent at 44–45 d old.

In comparison to an adjacent inland kestrel species, Seychelles and Mauritius kestrels, the nest success of 50% of Madagascar Kestrels was lower due to the predation on eggs and nestlings, inclement weather, and possibly the smaller sample size.

The Madagascar Kestrel's diet was reported to comprise mainly of insects and some vertebrates (Rand 1936, Cade 1982, Langrand 1990, Ferguson-Lees and Christie 2001). On Masoala Peninsula, the kestrel's diet during the breeding season was vertebrates, and predominantly terrestrial plated lizards (*Zonosaurus* spp.; 93.8%, $N = 317$). This was similar to the Seychelles Kestrel, which fed mainly on skinks (*Mabuya seychellensis*) and some day geckos, (*Phelsuma* spp.) and the Mauritius Kestrel, which consumed mostly day geckos (93%; Cade 1982, Jones 1984, Watson 1992). The sympatric Banded Kestrel studied in the same area also preyed on lizards, but more on arboreal species, such as chameleons (*Furcifer* and *Calumna* spp.) and day geckos (Rene de Roland et al. 2005).

In this study, almost half of the identified prey, 158 of 338 (46.7%), were captured during the nest-

ling period. The majority of prey was delivered by male Madagascar Kestrels (82.3%, $N = 130$) relative to females (17.7%, $N = 28$). Watson (1993) reported male Seychelles Kestrels increased their hunting effort during nestling period, delivering 92% of the food to the young.

In comparing the Madagascar Kestrel with the two other closely-related insular kestrels, the Seychelles and Mauritius kestrels, and the larger sympatric Banded Kestrel, this species seems to be adapted to open and disturbed habitats. Thus, the Madagascar Kestrel may have benefited from deforestation, human activities, and villages. Also, in comparison to the other two kestrels, the Madagascar Kestrel frequently hovers for hunting, has two color morphs, and has a relatively short breeding season. The Mauritius Kestrel is morphologically similar to an accipiter and its habits and behavior reflect this based on its occupancy of forested habitat, and the Seychelles Kestrel is found both in forested and open habitat (Cade 1982, Watson 1992).

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